Life history and behavioral responses to time constraints in a damselfly.

by Frank Johansson and Locke Rowe

Time constraints, imposed by seasonality, are common to life histories. Recent theory in evolutionary ecology predicts independent behavioral and life history responses to such constraints, but this theory remains largely untested. In our two experiments on the damselfly Lestes congener we experimentally alter individual's perception of their proximity to a time constraint and ask whether their behavior and life history respond in the directions predicted by theory. We altered larval perception of their position in the season with light regime. In one group, we hatched larvae from winter diapausing eggs in a light regime that mimics a relatively early time in the season. In the other group we hatched larvae in a light regime that mimics a late time in the season. In the late (time constrained) group, larvae would have very little time to complete development and reach a large size so that they could attain their full reproductive potential prior to winter. In the first experiment, the behaviors we assess are activity rate, which is an indicator of foraging effort and willingness to take risks, and cannibalism, which is a component of the mortality risk of foraging. As predicted, time-constrained larvae increased their activity rates, perhaps in an attempt to increase weight gain, and as a result they suffered higher rates of cannibalism. In the second experiment, we measured development rate as the rate of molting and age at maturity. As predicted, time-constrained larvae accelerated development rate and thereby matured at a significantly earlier age and smaller size. Our analysis demonstrates that the behavioral and life history responses of these larvae were independent, in the sense that the life history responses did not result from the behavioral responses.

Key words: cannibalism; damselfly; development; foraging; Lestes congener; life history; odonates; seasonality; time constraints; trade-offs.

INTRODUCTION

Time constraints on the life history, imposed by seasonality, are expected to be common in a wide variety of life history transitions (hatching, metamorphosis, maturation) and taxa (reviews in Roff 1980, Forrest 1987, Daan et al. 1989, Rowe and Ludwig 1991, Rowe et al. 1994). Consider a simple animal life history where eggs emerge from winter diapause, hatch into juveniles, grow, mature, and then produce overwintering eggs during a prolonged reproductive season. On one hand, larvae that do not mature prior to the onset of winter have a fitness of zero and those that mature with little time remaining in the season may not have enough time to produce their entire complement of eggs. On the other hand, accelerating maturity comes at a cost of a reduced period of growth and therefore typically reduced fecundity. Thus a trade-off exists between size and timing of this life history transition. The advantage of large size is relatively constant as the season progresses. However the relative cost to delaying maturation is ever increasing through the season; the cost of delaying one day on the day before the onset of winter is infinite! Therefore, we expect late individuals to trade off further growth against earlier maturation and size at maturity to decline as the season progresses. Indeed, this effect may explain the common pattern of seasonal declines in size at emergence in insects (Forrest 1987, Mousseau and Roff 1989, Rowe and Ludwig 1991), size at breeding in fish (Wiegmann et al. 1997), and in avian clutch size (Daan et al. 1989, Rowe et al. 1994).

The empirical evidence for a cost to late transitions between life history stages is accumulating. For example, in insects, birds, and fish, eggs produced earlier in the season often have higher recruitment than those produced later (e.g., Landa 1992, Wiggins et al. 1994, Cargnelli and Gross 1996), duration of reproductive period is correlated to lifetime fecundity in odonates (Banks and Thompson 1988, Fincke 1988), and late metamorphosing amphibians are at risk of pond drying (e.g., Wilbur 1980, Newman 1994, Skelly 1997). However, testing predictions of accelerated life history transitions under time constraints has been more difficult and often correlative (e.g., Daan et al. 1989, Mousseau and Roff 1989, Rowe et al. 1994). One of the more difficult empirical challenges to such tests is disentangling the effects of an individual's proximity to a time constraint from other environmental and phenotypic factors that are similarly correlated with time in the season. Individuals born late in the season may have accelerated development rates for a variety of reasons other than as a response to an impending time constraint. For example, food supply, predation risk, and maternally provided nutrition may all differ between early- and late-born individuals, and all of these factors may affect optimal development rates and behavior.

One commonly used approach has been to alter photoperiod, and thereby alter the test organism's perception of time remaining in the season, and to assess its effect on age and size at some life history transition (Dingle 1978, Tauber et al. 1986). Studies of univoltine insects have found that development is accelerated and in some cases size reduced in individuals that perceive an approaching time horizon, including odonates (Lutz 1968, 1974, Norling 1984), orthopterans (Masaki 1967, Carriere et al. 1996), and lepidopterans (Nylin et al. 1989, 1992, Leimar 1996). One problem with all of these studies is that light regime is set at the beginning of the experiment and then held constant. It is easy to imagine that this may exaggerate effects if levels are set very close to the time horizon, or minimize effects if they are set more distant from the horizon. Leimar (1996) has pointed to another important and potentially confounding factor to the interpretation of these studies. He notes that a good deal of the increase in development rate may have resulted from increased foraging effort in time-constrained individuals. Virtually all of the tests done on photoperiod effects on age and size at maturity suffer this problem because they do not monitor food intake, foraging effort, or growth rate. In Leimar's (1996) experiment, where he did monitor growth rate, he found that growth rate was not affected by photoperiod, and that accelerated development was limited to the later part of the final instar and the pupal stage. Nonetheless, his study like most, included abundant food supply in all light regimes. Hence it would not be surprising if growth rate were maximal in all photoperiods, which would preclude any need to increase costly foraging effort.

Several models of the effects of seasonal time constraints on foraging behavior predict costly increases in foraging effort as time horizons are approached. Foraging effort may be increased by switching habitats (Ludwig and Rowe 1990, Leonardsson 1991, Rowe and Ludwig 1991) or increasing foraging activity within a habitat (Houston et al. 1993, Werner and Anholt 1993, Abrams et al. 1996). These foraging shifts have the same underlying causalities as the shifts leading to the prediction of accelerated development as a time horizon approaches. For example, if some minimum size must be reached by the end of the season or fitness is an increasing function of reserves at the end of the season, then foragers are expected to increase foraging rates near the time horizon at the expense of increased predation rate. As noted by Leimar (1996) this behavioral response may affect growth rates and the life history response because growth and development may be coupled. Yet they may actually occur independently. Consider an adult that must accumulate a certain level of reserves to survive winter. No development is occurring here, but we still expect individuals with low reserves to increase foraging effort as the winter approaches. We are unaware of any direct tests of the effects of time constraints on foraging effort.

The predicted increase in foraging effort has the potential to affect many kinds of predator-prey interactions, including cannibalism. Cannibalism is present in many damselfly species (Johansson 1992, 1993, Anholt 1994, Fincke 1994) and has been suggested to be an important factor for larval mortality in the field (Wissinger 1989, VanBuskirk 1992). Cannibalism, the killing and consumption of conspecifics, may have important consequences for regulation and dynamics of populations (Polis 1980, Orr et al. 1990, Crowley and Hopper 1994). The three major factors determining the intensity of cannibalism are: density of conspecifics, density of alternative prey, and vulnerability of conspecifics, e.g., size differences (Dong and Polis 1992). A fourth could be the time of season. If animals are time constrained, individuals may increase risky foraging effort in an attempt to quickly gain mass. Cannibalism is an increasing function of activity rates (Johansson 1993); therefore, if time constraints increase activity, we expect a corresponding increase in cannibalism. Similarly, in nature we would expect increasing activity levels to increase noncannibalistic predation rates. Several studies have shown that activity rate is correlated with predation risk (reviewed in Werner and Anholt 1993).

In this paper, we conduct two experiments to test predictions concerning the behavioral and life history responses of the damsel fly Lestes congener to a time constraint imposed by their seasonal environment. We focus on foraging activity in the face of cannibalism, and on age and size at maturity. Odonates in the temperate region are well-suited for studying this problem. Some species, including Lestes congener, have 1-yr obligate life cycles and contracted breeding periods (Walker 1953). We should expect such species to have marked behavioral and developmental flexibility if subjected to time constraints. We predict that time-constrained individuals will increase activity rates, and pay for this by suffering higher cannibalism. We also expect time-constrained individuals to accelerate development to maturity. If growth rates are held constant between treatments, we also expect a decline in size at maturity in the rapid developers because of the familiar tradeoff between age and size at maturity. Several studies have shown that development in odonates is affected by light levels (e.g., Lutz 1968, Lutz 1974, Norling 1984). In each case, damselflies responded to light levels, and in an apparently adaptive manner. However, these studies were conducted for only a portion of the larval period, food supply was not controlled, and growth rate was not monitored.

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METHODS

We used the damselfly Lestes congener Hagen, as our study species. This species oviposits endophytically in the late summer and fall and overwinters as eggs (Walker 1953, Sawchyn and Gillott 1974a). Eggs hatch in spring, and larvae grow and mature to breed during the flight period that begins in early August and ends in early October (Walker 1941; E Johansson, personal observation). We take advantage of the overwintering of eggs in this experiment. Two groups of diapausing eggs, with the same history, can be hatched out at the same time with the same environmental conditions, other than light. This allows us to disentangle the effects of light from other components of the environment, maternal effects, and effects of egg age.

We collected eggs in September from a pond at Guelph, Ontario, by sampling stems of Poaceae and Typha spp. in which females had oviposited. Stems were held in the laboratory at room temperature and with natural light conditions until 15 November. They were then transferred to a climate chamber at a temperature of 5-6 [degrees] C and a light/dark cycle of 7.5:15.5 to mimic local winter conditions and arrest development in the eggs. On 3 January 1997, eggs were haphazardly divided into two groups, and placed into two large pools (35 x 28 cm with a depth of 13 cm) of water. We then placed each pool into one of our experimental light regimes, created in walk-in environmental chambers.

We set light levels at hatching to simulate those that would be experienced by larvae that had hatched early in the season and those that had hatched late in the season. In the wild, a good deal of variance probably exists in hatching dates among individual eggs within sites and between sites, because of micro- and macro-scale fluctuations in temperature and water levels. Lestes oviposit at different heights in stems that are often above water prior to spring melting. Postdiapause development of Lestes eggs can start at 0 [degrees] C, but does not start until the eggs are wetted as the pond fills with water (Sawchyn and Gilliot 1974a, b). We assumed a hatch to adult period of [approximately] 20 wk and then counted back from early in the flight period to set starting light conditions for early larvae, and similarly, from late in the flight period for late larvae. Earliest and latest observations of adult L. congener in Ontario are 9 August and 13 October, respectively (Walker 1941, [ILLUSTRATION FOR FIGURE 2 OMITTED]). This resulted in starting light regimes simulating 15 March (lights on 0627-1822) for the "early" treatment larvae and 1 June (0439-1948) for the "late" treatment larvae, conditions at the latitude of the study (Guelph, Ontario). Henceforth we refer to larvae from these two treatments as early and late (time constrained), respectively. The light was thereafter adjusted every week to simulate the progress of natural light condition. Temperature was 22 [degrees] [+ or -] 0.5 [degrees] C. With only two chambers and two light regimes, it is possible to conflate "chamber" and "light" effects. For example, some component of the environment other than light regime may differ between the chambers and thereby confound interpretation of our results. To remedy this problem, we rotated larvae and their respective light conditions through the two chambers on a 2-wk cycle.

After 4 wk (2 February) when all the larvae had hatched, they were transferred to experimental conditions for each of the two experiments described below. Therefore 2 February becomes day 0 for the experiments described below, and is also considered the day of hatching for estimates of development rate.

Experiment 1: cannibalism and activity

To determine the effect of a perceived time constraint on larval behavior we compared activity and cannibalism rates in groups of larvae held under the two light regimes. On 2 February, ten of the recently hatched larvae were introduced into each of 16 (eight replicates of two treatments) plastic containers (height 15.5 cm, diameter 20 cm) filled with 600 mL water. This corresponds to a density of 318 larvae/[m.sup.2], which is within the bounds reported in nature (Macan 1964, Duffy 1994). Larvae were hatched in the same light regime corresponding to the treatment in which they were used. Experimental containers had habitat structure consisting of two strips of fiberglass window screening (mesh size, 1 mm). Strips (30 cm long and 2 cm wide) were tied together to form a cross and placed centrally at the bottom of each container. Larvae were fed brine shrimp and protozoans every Monday, Wednesday, and Friday. Mean number of prey given per container was 263 [+ or -] 31 SE (based on six random samples). Hence, a mean rate of [approximately] 26 shrimps per individual under the assumption that all damselflies were alive. Once a week we checked the containers for dead or cannibalized individuals. If no sign of wounding or chewing was found on them, we assumed that they had died from causes other than cannibalism. Note that larvae do not feed on immobile prey (Pritchard 1965).

On day 30 and 55 we counted the number of larvae alive in the containers. By assuming that all missing individuals had been cannibalized and counting the number of corpses with evidence of cannibalism, we estimated the rate of

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cannibalism. Activity rate of larvae was estimated on a 2 x 2 cm grid, drawn on the bottom of the containers, on day 34 and 54. On each date, the position of one randomly chosen individual in each container was noted on the grid every 15 min between 0900 and 1200. Individuals could easily be distinguished by size and pigmentation. Activity rate was estimated as the number of times the individual had moved during these 3 h. These activity rates were measured on days in which no food was supplied. The experiment was terminated on day 55, when the head width (distance between outer margin of the eyes) of all remaining individuals was measured.

Experiment 2: development rates, and age and size at maturity

To determine the effect of time constraints on larval age and size at maturity, we compared age and size of adults emerged from larvae subjected to early and late (time constrained) light regimes. Larvae were housed in small plastic cups (height 7 cm, diameter 5.5 cm) containing 100 mL water. There were 28 cups per treatment, with one individual in each cup.

We used a food ration that was constant between treatments and resulted in below maximal feeding rates of larvae. Relatively low food rations were used to avoid the possibility of all larvae in each treatment developing at the maximal rate and therefore potentially obscuring treatment effects. We believe this also more closely resembles natural conditions, where food limitation of some damselflies has been suggested (Pickup et al. 1984, Baker 1988, Anholt 1990a, McPeek 1998). We held feeding regime constant between treatments so that any treatment effects could be attributed directly to light regime rather than to indirect effects of light on feeding rate. We used three feeding regimes as larvae aged. During the first 28 d of development, larvae were fed a fixed

ration of protozoa from a laboratory culture, and a fixed ration of brine shrimp (63 [+ or -] 7.9 SE) every Monday, Wednesday, and Friday. The brine shrimp ration continued until day 82. Throughout this 82-d period brine shrimp were rarely found dead at the bottom of containers. Brine shrimp die within a few hours of exposure to freshwater, and larvae feed only on live prey. Therefore, we can conclude that all instars were able to consume brine shrimp. We do not know how many of the protozoa were consumed during this brief period. This feeding regime ensured that larvae were potentially satiated on only 3 of every 7 d of the week. Visual inspection of their gut revealed that they were empty on intervening days. For larger larvae (developmental day 82 onward) the brine shrimp ration was replaced with one worm (Enchytritraeidae: from laboratory culture) on each of 5 d per week until they emerged. This ration had a dry mass 2.5 times that of the brine shrimp ration.

We used two indices of developmental rate: molting rate and age at maturity. To estimate the molting rate of larvae, cups were checked daily for larval exuviae. Molting rate was calculated as the number of molts completed over a given period (see Methods: Analysis). We also used these data to determine if the treatment had any effect on the total number of instars completed prior to emergence. As larvae emerged, adults were sexed and weighed. Mass at maturity was determined by weighing individuals following drying at 60 [degrees] C for 48 h. Our estimate of growth rate was the size at maturity divided by the age at maturity.

Analysis

We used multivariate analysis of variance (MANOVA) to determine if there were significant overall effects of light regime on the response variables age at maturity, size at maturity, instar number, molting rate, and growth rate. Here we calculated molting rate as the total number of molts completed in the larval period divided by age at maturity. Subsequent univariate ANOVAs were used to elucidate which responses contributed to the significant multivariate response. Repeated measures (sampling date) ANOVAs with containers as the sampling unit were used to determine if there were differences in activity and cannibalism between early and late individuals in the cannibalism experiment. We use repeated measures ANOVA similarly for analysis of molting rate on the three dates that we calculated it (day 0-30, 31-55, and 6192). Here, analyses were conducted on the number of molts that had passed since the last sampling date. Deviation from normality was tested with Kolmogorov-Smirnov (Lilliefors) test and homogeneity of variance with Bartletts test. All statistical analyses were performed in SYSTAT (Wilkinson 1988).

RESULTS

Cannibalism and activity

Late larvae were almost twice as active as those in the early light regime [ILLUSTRATION FOR FIGURE 1A OMITTED]. A one-way repeated measures ANOVA on activity of individuals with date of activity measurement as the repeated measure and light regime as the factor revealed a significant effect of light regime (MS = 157.53, [F.sub.1,14] = 65.96, P [less than] 0.001). No effect of date (MS = 0.03, [F.sub.1,14] = 0.006, P = 0.94), or the interaction between date and light was found (MS = 1.53, [F.sub.1,14] = 0.29, P = 0.60). It is interesting to note that activity rates continued at higher rates through much or all of the larval period despite the fact that increased activity would not have increased foraging returns in the design that we employed (all food was consumed in each treatment).

Cannibalism was about two to three times greater in late than early larvae [ILLUSTRATION FOR FIGURE 1B OMITTED]. A one-way ANOVA on number of individuals cannibalized with measurement date as a repeated measure and light regime as the factor revealed a significant effect of light regime on cannibalism (MS = 28.12, [F.sub.1,14] = 30.88, P [less than] 0.001). There was no significant effect of date (MS = 3.00, [F.sub.1,14] = 0.78, P = 0.392) or the interaction between light and date (MS = 3.13, [F.sub.1,14] = 1.22, P = 0.288). Mean head width (mm) of surviving individuals in a container was significantly greater (t test; t = 8.81, P = 0.001) in the late (high cannibalism) treatment (mean [+ or -] 1 SE, 2.6 [+ or -] 0.10) than in the early (low cannibalism) treatment (1.79 [+ or -] 0.04). Similarly, the mean head width size of the largest individual in each light regime differed significantly (t test; t = 7.11, P [less than] 0.001) between late (2.7 [+ or -] 0.06) and early larvae (2.15 [+ or -] 0.05).

Molting rate, and age and size at maturity

There were a total of 24 individuals that survived to maturity in the late treatment and 17 in the early treatment. A MANOVA indicated that light regime had a strong impact on life history traits and that males and females responded in similar ways (Table 1). Late larvae had an earlier age at maturity, an elevated molting rate, a smaller size at maturity, and reduced growth rate. Fig. 2 expresses these data with respect to the calendar dates that we simulated with our light treatment. This figure shows the decline in size at maturity in later, faster developing larvae. The figure also illustrates that we were successful with our light regimes in creating larvae that emerged early in the season and late larvae that were approaching the end of the breeding season and were, therefore, time constrained.

Two factors indicate that differences in growth rate between the treatments were small or nonexistent. First, when growth rate is calculated in the form ln(mass at maturity)/age at maturity rather than mass at maturity/age at maturity, as we have here, the growth rate term becomes insignificant (P = 0.428), without changing the significance of other effects. Second, following the conservative application of sequential Bonferroni adjustment for multiple tests to the data in Table 1, only the effects on age and size at maturity remained significant. Nevertheless, we will remain open to the view that there may have been a small change in growth rate and this independently affected age and size at maturity.

Both indicators of development rate (age at maturity and molting rate) showed a significant effect of light regime [ILLUSTRATION FOR FIGURES 3A, B OMITTED] in univariate analyses. There was no significant effect of light regime on the total number of molts completed by maturity (Table 1). Therefore, late larvae simply accelerated the rate that they passed through these molts on the first two of three sampling dates [ILLUSTRATION FOR FIGURE 4 OMITTED]. This result was supported by a one-way repeated-measures ANOVA on the number of molts completed between each sampling date, with the three sampling dates as the repeated measure and light regime as the factor. This analysis revealed no significant effect of light (MS [less than] 0.001, [F.sub.1,44] [less than] 0.001, P = 0.993), but a significant effect of date (MS = 37.55, [F.sub.1,44] = 57.14, P [less than] 0.001) and the interaction between light and date (MS = 2.381, [F.sub.2,88] = 8.13, P [less than] 0.001). Hence, late larvae went through their instars faster than early individuals, but early individuals caught up in instar as emergence approached. Each instar of damselflies increases in duration, creating the possibility for this catch-up effect as development proceeds (Lawton et al. 1980, Dixon and Baker 1987).

TABLE 1. MANOVA and ANOVAs on Lestes congener larval developmental days, instar number, size (mg) at emergence, total molting rate, and growth rate.

Source	df	Wilks' lambda	F	P
MANOVA				

Light regime	5, 30	0.424	8.152	[less than]0.001
Sex	5, 30	0.952	0.302	0.908
Light regime x Sex	5, 30	0.941	0.375	0.862
ANOVAs				
Age at maturity				
Light regime	1		37.316	[less than]0.001
Sex	1		0.001	0.977
Light regime x Sex	1		0.101	0.752
Error	37			
Instar number				
Light regime	1		0.001	0.974
Sex	1		0.334	0.567
Light regime x Sex	1		0.656	0.423
Error	37			
Size at emergence				
Light regime	1		19.042	[less than]0.001
Sex	1		0.755	0.391
Light regime x Sex	1		1.105	0.301
Error	34			
Molting rate				
Light regime	1		4.110	0.050
Sex	1		0.325	0.572
Light regime x Sex	1		0.445	0.509
Error	37			
Growth rate				
Light regime	1		5.127	0.030
Sex	1		0.895	0.351
Light regime x Sex	1		0.593	0.447
Error	34			

Notes: Factors were light regime and sex. The degrees of freedom are lower for growth rate and size because some larvae became trapped in their exuviae during the final molt, precluding measurement of final size.

The first few instars are completed very quickly, and we may have therefore missed one to two molts during the hatching period. We could detect no molting in the hatching containers and no difference in size of larvae between treatments. Nevertheless, it remains possible that some accelerated development of late larvae occurred during our hatching period. However, if this were so, it represents a minor portion of development. First, we have recorded accelerated development for long after this period [ILLUSTRATION FOR FIGURE 4 OMITTED]. Given that instar duration increases with each passing instar, if larvae from the late treatment had passed more molts in the hatching containers than did those from early treatments, we would expect slower molting rates in the posthatch period in late treatment. This is the opposite of what we found [ILLUSTRATION FOR FIGURE 4 OMITTED]. Second, the total number of instars completed during the posthatch period (Day 0 onward) did not differ between late and early treatments (Table 1). If larvae from the late treatment had passed more molts in the hatching containers than did those from early treatments, then they must have had a greater number of instars over their lifetime than did those in the early treatment. This seems unlikely because it would require that larvae responded to an approaching time horizon by increasing the number of molts prior to maturity, while decreasing both the age and size at maturity.

The significant reduction of body size (24%) at maturity for late larvae [ILLUSTRATION FOR FIGURE 5A OMITTED] resulted from two factors. First, there was an 11% but insignificant reduction in growth rate [ILLUSTRATION FOR FIGURE 5B OMITTED], and second, age at maturity was significantly reduced (11%, [ILLUSTRATION FOR FIGURE 3A

OMITTED]). Thus, late larvae attained any one size at a marginally later time than early larvae, but were developing at a much faster rate and thus matured at a smaller size. Fig. 6a shows a plot of individual age at maturity on growth rates of those individuals. It is clear that there was a good deal of overlap between growth rates of larvae in the two light regimes, but late larvae had an earlier age at maturity for any one growth rate. In the zone of overlap in growth rates, mean age at maturity of late larvae was reduced relative to early larvae (t = 6.03, df = 17, P [less than] 0.001). Thus, the smaller size at maturity for late larvae resulted, in part, from their more rapid development rate [ILLUSTRATION FOR FIGURE 6B OMITTED]

DISCUSSION

Our results demonstrate that Lestes congener larvae respond to time constraints by accelerating development and increasing activity rates, as predicted by theory. The life history and behavioral responses are independent in the sense that increased development rates did not result directly from an increase in growth associated with increased food consumption. Thus, faced with a time constraint, larvae accelerated activity and development rates, and paid for this with increased exposure to cannibalism, and decreased size at maturity. These results support the key predictions from recent theory on the effects of time constraints on the life history and on foraging behavior.

Activity rates and cannibalism

Activity rate of late larvae was nearly twice as high as early larvae [ILLUSTRATION FOR FIGURE 1A OMITTED]. This is a particularly strong result because the demographic forces acting in this experiment are expected to dilute this effect as the experiment progresses. Specifically, cannibalism in the late treatment reduced relative density and increased per capita food supply. We may expect both factors to lead to reduced activity by prey and predators. As predicted, increased activity resulted in increased cannibalism rates on those same dates [ILLUSTRATION FOR FIGURE 1B OMITTED]. Similarly, this is a strong result because of demographic changes in the late treatment. Increased per capita food supply for late larvae ought to decrease hunger of cannibals and therefore their rate of cannibalism as the experiment progressed. Mean size of remaining larvae was greater in the late treatment. This is an expected result because of both increased per capita food supply and the nutrition gained from cannibalism.

Our design does not allow us to determine whether increased susceptibility (due to increased activity levels), increased propensity to cannibalize, or a combination of these led to the observed increase in cannibalism. We suggest that both factors operate. Johansson has shown that cannibalism increases in damselflies as the cannibals increase their activity (Johansson 1992), and as prey increase their activity (Johansson 1993). Moreover, had we had predators of damselflies in the containers, we would expect predation rates to increase. Previous studies have shown that predation rate on damselflies is an increasing function of activity rates of damselflies (McPeek 1990, Johansson 1993). This could be tested in the future by directly assessing risk taking in larvae exposed to predators under early- and late-season light conditions. Nevertheless, it is clear that mortality risk is an increasing function of activity rate, and that the time-constrained (late) larvae were more willing to take this risk than were early larvae.

Odonates are often the top predators in fishless systems, hence, cannibalism together with intraguild predation may be a mortality factor for odonates in such systems (Robinson and Wellborn 1987). On the other hand, if fish are present, cannibalism may become less important than fish predation. Although we studied mortality as cannibalism, the increased foraging effort of late individuals might result in high mortality in fish systems as well since actively foraging odonates are vulnerable to fish predators (McPeek 1990). Many other studies on cannibalism emphasize the density-dependent effects of cannibalism and its consequences on population dynamics (Polis 1980, Orr et al. 1990). We show here that cannibalism may increase without such density-dependent effects. Likewise, our results are a rare example of the proposed connection between individual behavior and population dynamics (Anholt 1997). We have manipulated individual behavior (activity rate) independently of density and shown a response in a population parameter (mortality rate).

Two central predictions from theory that connects foraging behavior to life history are first, that risk taking will be condition dependent, and second, that risk taking will increase as individuals approach a time constraint (e.g., Mangel and Clark 1986, Ludwig and Rowe 1990, Leonardsson 1991, Rowe and Ludwig 1991, Clark 1993, Houston et al. 1993, Werner and Anholt 1993, Abrams et al. 1996). The two hypotheses are connected. Consider a prereproductive individual that must reach adulthood with a certain level of stored fat prior to winter to survive. Near the onset of winter, we would expect increased foraging effort and risk taking in those individuals that had not stored the required fat. To not do so would lead to a fitness of zero. Previous studies have confirmed the first prediction, that risky or otherwise costly foraging is condition dependent (e.g., Milinski and Heller 1978, Dill and Fraser 1984, Kohler and McPeek 1989, Rowe et al. 1996). However, support for the second prediction is lacking. Lestes larvae must grow to maturity to reproduce before winter because diapause occurs in the egg stage, and we expect that earlier maturating larvae will be able to achieve a higher proportion of their potential. In support we show that individuals closer to the time horizon (late) increased their activity rates relative to those more distant from the time horizon (early).

Life history models for age and size at maturity typically assume a fixed growth rate in a given size or stage (reviewed in Roff 1992, Stearns 1992, Abrams and Rowe 1996). More recent models include the potential for individuals to adjust their growth rate by switching habitats (Werner and Gilliam 1984, Ludwig and Rowe 1990, Rowe and Ludwig 1991, Houston et al. 1993) or by adjusting foraging effort within a habitat (Abrams et al. 1996, Abrams and Rowe 1996). Of the models that deal with time constraints, each predicts that individuals may increase growth rate in response to an approaching time horizon. Increased growth clearly may accelerate development independently of any direct response to a time constraint. Leimar (1996) has pointed out that ability to adjust growth rates has not been considered in most of the several previous tests of the effects of photoperiod on age and size at maturity and that this has confounded interpretations of results. Our study makes two contributions here. First, it suggests that faced with a time constraint on the life history, organisms do increase foraging effort as indicated by the increased activity rates observed here. Second, we have shown that late larvae increase development rate (reduced age at maturity) independent of growth rate.

Age and size at maturity

As predicted, larvae faced with a time constraint increased their development rate and as a result were smaller at maturity [ILLUSTRATION FOR FIGURES 2 AND 3 OMITTED] This acceleration in development is expected from theories of time-constrained univoltine life histories (Forrest 1987, Rowe and Ludwig 1991, Rowe et al. 1994). If growth rate is constant through the season, we therefore expect a seasonal decline in size at maturity as we have observed here (compare our [ILLUSTRATION FOR FIGURE 2 OMITTED] with [ILLUSTRATION FOR FIGURE 1 OMITTED] in Rowe and Ludwig 1991). Notably, such seasonal declines occur in damselflies (Anholt 1990b, Gribbin and Thompson 1991), although we are unaware of a relevant study of Lestes. In short, there are typically fitness advantages of large size (e.g., fecundity, mating success) that are counterbalanced by the advantages of early maturation. As the season progresses, the relative costs of late maturity increase, but the advantages of large size may remain constant. Therefore, we expect accelerated development rates for late relative to early individuals. In a univoltine life history, advantages of early maturation may include an increased reproductive period (offspring number) and an increased quality of those offspring. Given that these two correlates of fitness interact multiplicatively, the fitness benefit of early maturity can be substantial. Lestes congener is univoltine with winter diapause in the egg stage, which is common among temperate Lestes spp. (Sawchyn and Gillott 1974a, b). There are three potential advantages of early emergence. First, it is clear that emergence must occur prior to winter because larvae cannot overwinter. Second, duration of the reproductive period is typically associated with fitness. The longer the duration, the greater the fecundity for females and the greater the mating success for males (Banks and Thompson 1988, Fincke 1988). Third, Lestes eggs must undergo partial development prior to diapause; therefore, the latest eggs will not achieve this prior to winter.

Although fitness is a function of body size in many insects (Thornhill and Alcock 1983, Roff 1992), evidence for an effect of adult body size on fitness in damselflies is sparse and contradictory. Directional selection for large size, for small size, and stabilizing selection on size have all been reported for a variety of correlates of fitness in damselflies (Banks and Thompson 1988, Fincke 1988, Anholt 1991, Michiels and Dhondt 1991, Cordero 1995). There have been no studies of body size effects on fitness in Lestes congener. Our results are those expected for an advantage of large size in both sexes. If it is the case that there is no advantage of large size, then it is puzzling that the early individuals delayed emergence relative to late individuals, given a clear advantage of early maturation. One alternative is that there is a physiological cost of rapid development. If this is the case, then there is a life history trade-off between the physiological costs of rapid development and the reproductive advantages of early maturation. The effects of time constraints on developmental rate are, nevertheless, the same as those outlined earlier: the relative cost of delayed maturation increases as the season progress; therefore, we expect accelerated development late in the season.

We note that the reduced growth rate observed in late individuals, although not statistically significant, has the potential to confound our results. First, it suggests that our feeding regime did not equalize growth rates between early and late individuals as we had intended. Although feeding regime was equal between treatments, the switch to higher food level at day 82 may have led to reduced growth in the late relative to early individuals. Because of the accelerated development of late larvae, they spent a lower proportion of their larval period under this higher food ration. More problematic is the fact that, under some assumptions, reduced growth rates are expected to lead to increased development rates (reviews in Roff 1992, Abrams and Rowe 1996). Three lines of evidence suggest that the marginally reduced growth rates of late individuals do not explain their accelerated development. First, previous studies of damselflies have consistently shown that development rate is accelerated at high rather than low food levels (e.g., Lawton et al. 1980, Baker 1982, 1988, Pickup and Thompson 1984, 1990, Anholt 1990a). Second, development rate of late larvae was accelerated well before the change in ration [ILLUSTRATION FOR FIGURE 4 OMITTED]. Third, it is clear that in the zone of overlap between growth rates of late and early individuals, development rate was accelerated in the late individuals [ILLUSTRATION FOR FIGURE 6A OMITTED].

Conclusion

We have shown that larvae of Lestes congener, faced with the perception of an approaching time horizon, adjust their behavior and life history in a direction that is predicted by theory. Time constraints such as those discussed above are probably as ubiquitous as seasonal life cycles (Rowe and Ludwig 1991). The ontogeny of organisms is marked by a series of transitions between stages (egg to larvae, metamorphosis, juvenile to adult), and these transitions are typically localized to seasons. Seasonality implies that there is a good time and a bad time for transitions to occur, and hence a time constraint is imposed. We, therefore, expect that the behavioral and life history responses to time constraints that we have documented here will be very common. The key to future tests is to find an appropriate cue that organisms use to assess their proximity to a time constraint, and then to assess behavioral and life history responses to that cue. There is a relatively long tradition of using this approach in the study of life history timing, but it is only beginning in studies that connect foraging behavior to life histories.

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